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Vestibular–Somatosensory Interactions: A Mechanism in Search of a Function?

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Abstract

No unimodal vestibular cortex has been identified in the mammalian brain. Rather, vestibular inputs are strongly integrated with signals from other sensory modalities, such as vision, touch and proprioception. This convergence could reflect an important mechanism for maintaining a perception of the body, including individual body parts, relative to the rest of the environment. Neuroimaging, electrophysiological and psychophysical studies showed evidence for multisensory interactions between vestibular and somatosensory signals. However, no convincing overall theoretical framework has been proposed for vestibular–somatosensory interactions, and it remains unclear whether such percepts are by-products of neural convergence, or a functional multimodal integration. Here we review the current literature on vestibular–multisensory interactions in order to develop a framework for understanding the functions of such multimodal interaction. We propose that the target of vestibular–somatosensory interactions is a form of self-representation.

Keywords

Vestibular system; multisensory integration; somatosensory perception.

1. Bridging Phenomenology and Anatomy

The vestibular system plays an essential role in everyday life, contributing to a surprising range of functions from reflexes to the highest levels of perception and consciousness. Three orthogonal semicircular canals detect rotational movements of the head in the three-dimensional space (i.e., pitch, yaw and roll), and two otolith organs (utricle and saccule) sense translational acceleration, including the gravitational vertical. The importance of these vestibular signals for behaviour is self-evident, since almost all coordinated interactions with the external world involve some movements of the organism with respect to the environment.

How the same signals contribute to our perceptual awareness of the environment is less clear. Indeed, in normal sensorimotor coordination, it is hard to identify a distinctive vestibular phenomenology. What the literature often discusses as ‘*vestibular sensations*’, such as vertigo, can, in fact, be seen as interoceptions of the systemic consequences of extreme, or unusual, or unexpected vestibular signals. Moreover, most of the events detected by the vestibular system are also detected by other sensory systems, notably visual and proprioceptive systems. The perceptual experience of head rotation and acceleration is normally a synthetic result of mixing multiple redundant cues (Angelaki and Cullen, 2008). Phenomenal access to ‘*raw*’ vestibular sensation is questionable. The acceleration due to gravity transduced by the otoliths is a case in point. The signal is always on, but it is difficult to point to a specific phenomenal experience of gravity driven by this signal.

Vestibular inputs are strongly integrated with signals from other sensory modalities, such as vision, touch and proprioception (Faugier-Grimaud and Ventre, 1989). This convergence perhaps reflects the importance for survival, and the redundancy with other systems, described above. Multimodal convergence has been described in almost all vestibular relays, including the vestibular nuclei, the thalamus and several areas in the cerebral cortex (Lopez and Blanke, 2011; Lopez *et al.*, 2012; Zu Eulenburg *et al.*, 2012). The evidence for this convergence comes from two main sources. On the one hand, neuroimaging studies have revealed a functional anatomy of vestibular cortical projections. These studies, which we review in detail below, have identified brain areas activated or deactivated by vestibular stimulations using fMRI and PET. For instance, inhibitory vestibular–visual interactions fundamental in maintaining and controlling gaze evoked not only an activation of the parietal vestibular areas but also a decrease in rCBF of the visual cortex (Brandt *et al.*, 1998; Deutschländer *et al.*, 2002; Wenzel *et al.* 1996). On the other hand, electrophysiological studies have recorded single neurons responses to vestibular stimuli in areas such as the parieto-insular vestibular cortex (PIVC) (Grüsser *et al.*, 1990), the somatosensory cortex (Schwarz and Fredrickson, 1971) and the ventral intraparietal area (Bremmer *et al.*, 2002). The human homologue of the primate PIVC may not be a single area, so much as a distributed set of regions including the posterior and anterior insula, temporoparietal junction, superior temporal gyrus, inferior parietal lobule, and somatosensory cortices (Lopez and Blanke, 2011; Lopez *et al.*, 2012; Zu Eulenburg *et al.*, 2012). These studies identified neurons responding to combinations of tactile, visual and vestibular inputs, confirming the multisensory nature of the vestibular cortical network.

The predominant theme in recent electrophysiological work has been the convergence between vestibular information and vision for perception of self-motion, spatial orientation and navigation in the environment. In particular, vestibular–visual interactions are often interpreted within the framework of optimal cue combination, for multisensory perception of a single underlying quantity, namely one’s own heading direction (Fetsch *et al.*, 2009). However, there is growing evidence for multisensory interactions also between vestibular and somatosensory signals from both neuroimaging (Bottini *et al.*, 1994, 1995, 2001; Fasold *et al.*, 2002), and electrophysiological (Bremmer *et al.*, 2002) techniques.

2. What are Multisensory Interactions for?

Large bodies of recent neuroimaging and electrophysiological evidence are consistent with a general framework of vestibular–multisensory interactions. However, neither neuroimaging nor electrophysiology, in themselves, are conclusive regarding *function* of these interactions. Neuroimaging responses to artificial vestibular stimulation identify the existence of a projection, but do not clarify what it does. For example, the neuroimaging results showing somatosensory activations to vestibular stimulation are consistent with independent somatosensory and vestibular populations of neurons in the same cortical area, but not interacting (Bottini *et al.*, 1994, 1995, 2001; Fasold *et al.*, 2002). Electrophysiological studies confirm that a specific physical quantity, e.g., heading direction, is coded in the central nervous system (Grüsser *et al.*, 1990). However, recordings from single neurons cannot, in themselves, show how that code contributes to behaviour.

In recent years, the combination of extensive single-unit recording, and explicit computational theory has allowed strong and convincing functional accounts linking neural firing to behaviour. The successful integration of multiple sensory cues has been proven to be essential for precise and accurate perception and behavioural performance (Fetsch *et al.*, 2012). For example, the interaction between vestibular and visual signals has been interpreted as optimal intermodal combination of cues for heading (Fetsch *et al.*, 2009, 2012).

3. Self-Representation as a Target of Vestibular–Multisensory Interactions

In contrast, no convincing overall theoretical framework has been proposed for vestibular–somatosensory interactions, even though neuroimaging data has repeatedly identified an anatomical substrate for the interaction between vestibular and somatosensory signals (Bottini *et al.*, 1994, 1995, 2001; Fasold *et al.*, 2002), and perceptual studies have repeatedly shown phenomenological and perceptual effects of vestibular inputs on somatosensory measures (Bottini *et al.*, 1995; Vallar *et al.*, 1990, 1993; Ferrè *et al.* 2011a, b). However, it remains unclear whether such percepts are by-products of neural convergence, or a functional multimodal integration.

Why have functional accounts of vestibular–somatosensory interaction made less progress than functional accounts of vestibular–visual interaction? In our view, this is because we lack a candidate for the physical quantity that is the *target representation* for vestibular–somatosensory interactions, analogous to heading direction in vestibular–visual interactions. Because the end-product of vestibular–somatosensory interactions is unclear, functional theories and explicit computational models are lacking. In this paper, we review the current

literature on vestibular–multisensory interactions in order to develop a framework, or a sketch for a future functional theory, for vestibular–somatosensory interactions.

In a nutshell, we propose that the target representation of vestibular–somatosensory interactions is a form of self-representation. This representation has the role of linking the spatial description of one’s own body to the spatial description of the outside world. The heading direction emerging from vestibular–visual interactions would thus be one, specific instance of a linkage between the animal’s own body and the external environment, embedded in a general network of tactile, nociceptive and other mechanisms for coordination of simple sensorimotor interactions. Importantly, the vestibular–visual interaction is essentially cyclopean, serving to navigate a point organism through a spatially-extensive world. In contrast, the vestibular–somatosensory interaction involves the spatial geometry of the body itself as a volumetric object.

4. Which Forms of Multisensory Interaction Could Contribute to Self-Representation?

Haggard *et al.* (2013) have recently distinguished three different forms of multisensory interaction. The first is *feedforward multisensory convergence*, in which afferents carrying information in two distinct modalities converge on a single higher-order neuron. The higher-order neuron responds to stimulation in either modality, and is thus ‘bimodal’. The second involves transformation of information from one modality into the *spatial reference frame* of another. Such transformations involve a change in spatial tuning, but may not produce any overall change in neural firing rate. The third form of multisensory interaction is modulation by one sensory signal of the *gain* in a second sensory pathway. Accordingly, information in one modality is used to change synaptic connections in the afferent pathway of another modality.

Our concept of vestibular–multisensory self-representation could involve all three forms of multisensory interaction. We give simple illustrations here, with the aim of showing that self-representation is not a reflexive, or a transcendental cognitive function, but could be accommodated within current computational frameworks about multisensory processing. First, vestibular signals from the canals converge with visual information for optimal feedforward computation of gaze and heading. Second, gravity-dependent signals from the otolith organs, could provide an absolute reference frame for spatial representation, into which other internal and external information is transformed (Angelaki and Cullen, 2008). Third, gain regulation within different sensory pathways could flexibly balance the self-

environment interaction towards the proximal environment surround the organism's own body (e.g., boosting cutaneous sensation), or towards the distal environment (e.g., boosting visual transmission).

Here we review the recent literature with a view to bridging the phenomenology-anatomy gap for vestibular and somatosensory systems. We develop an overall position of vestibular-multisensory interactions as a key element of self-representation, and vestibular-somatosensory interactions as a specific contribution to bodily self-awareness. To reach this view, we group current knowledge about vestibular-somatosensory interactions into three broad classes: vestibular contributions to sensorimotor control, vestibular effects on spatial attention and cognition and vestibular modulation of somatosensory afference.

5. Vestibular–Somatosensory Interactions: Vestibular Contribution to Sensorimotor Control

The vestibular system does not fit the classical model of a modality-specific, dedicated sensory pathway, such as vision and touch. Instead, multisensory convergence between vestibular and somatosensory signals has been described at several levels in the central nervous system. These multisensory interactions occur for instance at the primary relay station of the vestibular signals, the vestibular nuclei, where more than 80 % of neurons are influenced by kinaesthetic afferents (Fredrickson *et al.*, 1966). However, the majority of neurons reported to respond to both vestibular and somatosensory signals have been found in the cerebral cortex. Fredrickson *et al.* (1966) recorded the cortical potentials evoked by direct electrical stimulation of the vestibular nerve in the rhesus monkey. The results showed a vestibular-responsive area in the posterior part of the postcentral gyrus, close to the intraparietal sulcus, and located between the primary and secondary somatosensory cortex (Brodmann's area 2). More importantly, single-unit recording showed that neurons in this area responded not only to vestibular stimulation but also to stimulation of the somatosensory median nerve (Fredrickson *et al.*, 1966). This evidence suggested an interaction between vestibular and somatosensory afferents within area 2. Later studies localised the site of the multisensory convergence in an area located posteriorly to area 2v (Fredrickson and Rubin, 1986; Schwarz and Fredrickson, 1971; Schwarz *et al.*, 1973). These data are additionally supported by results showing cortical responses evoked by peripheral stimulation of the vestibular receptors in monkey (Büttner and Büttner, 1978) and cat somatosensory area 2v (Jijiwa *et al.*, 1991).

Guldin and Grüsser (1998) estimated that about 30–50% of neurons in the somatosensory area 3aV receive vestibular inputs. Vestibular projections reach the primary somatosensory representation of the forelimb (Ödkvist *et al.*, 1973, 1974, 1975), the area coding for the neck and the trunk representations and extend anteriorly into the primary motor cortex (Akbarian *et al.*, 1994; Guldin and Grüsser, 1998; Guldin *et al.*, 1992). Most authors assume that vestibular–somatosensory neurons play some role in sensorimotor postural control. Schwarz and Fredrickson (1971) claimed that “*central convergence of these two modalities [vestibular and somatosensory] is apparently essential not only for lower reflex mechanisms but also for the conscious perception of position and movement*”, suggesting that the multisensory convergence between vestibular and somatosensory signals might be functional for balance responses and motor control. Successive electrophysiological studies supported this explanation describing the vestibular–somatosensory interaction as an adaptive bimodal response for maintaining postural reflexes and for controlling the position of body parts in external space (Fredrickson and Rubin, 1986; Schwarz *et al.*, 1973).

The link between vestibular–somatosensory interaction and postural responses has been described in many situations in humans. For instance, vestibular inputs are critical for initiation of postural responses to head and body displacements (Horstmann and Dietz, 1988). Critically, vestibular–somatosensory interactions vary with the context in which stimuli are presented and with the qualities of the stimuli. While vestibular inputs have little effect when surface somatosensory information predominates, vestibular signals greatly influence lower extremity motor outputs when somatosensory information is unavailable or unstable (Horak *et al.* 1994). This pattern of results suggests that vestibular and somatosensory systems provide alternative, complementary information relevant for postural control. Integrating these signals would thus potentially provide optimal postural control.

6. Vestibular–Somatosensory Interactions: Vestibular Effects on Spatial Attention and Cognition

The first description of the influence of vestibular stimulation on somatosensory processing in human was reported by Vallar and colleagues in 1990 (Table 1) (Vallar *et al.*, 1990). In three right-brain-damaged patients, the irrigation of the left ear canal with cold water (caloric vestibular stimulation) temporarily ameliorated left tactile imperception (hemianaesthesia) and many manifestations of the syndrome of left spatial neglect (Vallar *et al.*, 1990). Critically, the mirror-reversed paradigm, i.e. right ear cold caloric vestibular stimulation in

right hemianaesthesia has been unsuccessful so far (Vallar *et al.*, 1993; Bottini *et al.*, 2005). Such hemispheric differences suggest that left hemianaesthesia in right brain-damaged patients was a manifestation of inattention for the left side of space (Vallar *et al.*, 1990, 1993). Accordingly, the temporary remission induced by vestibular stimulation was due to vestibular activation of an attentional orientation mechanism. Specifically, vestibular stimulation caused a shift of attention toward the neglected side of the space/body, partly restoring its normal representations (Vallar *et al.*, 1990, 1993).

It has been recently described that galvanic vestibular stimulation modulates tactile extinction (inability to process or attend to the contralesional stimulus when two stimuli are simultaneously presented) in right brain damaged patients. The quality of remission of tactile extinction is polarity-specific (Table 1) (Kerkhoff *et al.*, 2011; Schmidt *et al.*, 2013). Interestingly, a repeated number of galvanic vestibular stimulation sessions can induce significant changes in tactile extinction that remain stable for several weeks. Although these studies provided some insights for rehabilitation, no clear functional explanation of such long lasting effects has been provided. Instead a range of different explanations can be hypothesised, including vestibular-induced changes in attentional mechanisms to recovery of an altered or damage body representations. The current consensus view regarding these clinical observations favours the idea that vestibular remission from apparently ‘primary’ sensory deficits, such as hemianaesthesia or tactile extinction, may in fact be an attentional phenomenon (Miller and Ngo, 2007; Utz *et al.*, 2010, 2011).

Effects of vestibular stimulation on attention have been extensively described. As early as 1941, Silberfenning (Silberfenning, 1941) suggested that the vestibular system plays a role in the spatial allocation of attentional resources. Rubens (1985) applied caloric vestibular stimulation to the auditory canal of the left ear in right brain-damaged patients with hemispatial neglect, and observed a transient improvement. He interpreted this recovery as reflecting low-level visual–vestibular interactions arising because the vestibular-induced nystagmus leads to direction-specific changes in visual input (Rubens, 1985). However, this explanation has been challenged by several clinical reports. Rorsman and colleagues (1999) reported a reduction of the attentional bias in visuo-motor tasks during galvanic vestibular stimulation. Similarly, vestibular stimulation decreases attentional bias in the bisection task (Utz *et al.*, 2011) and visuospatial constructive deficits in the Rey figure (Wilkinson *et al.*, 2010). These findings suggest an effect far beyond a mere by-product of vestibular–oculomotor reflexes, and instead affecting cortical mechanisms of visuospatial cognition. In the specific case of visuospatial attention, vestibular stimulation causes both modulations of

attentional bias in neurological patients (Vallar, 1990; Bisiach *et al.*, 1991; Bisiach *et al.*, 2000; Cappa *et al.*, 1987; Rode and Perenin, 1994), and reports of contralateral cortical activation, suggesting a direct interaction with a cortical locus. More recently, similar modulations of spatial attention have been reported in healthy participants receiving galvanic vestibular stimulation (Ferrè *et al.*, 2013a).

However, vestibular stimulation may have direct effects on somatosensory processing, in addition to changes in spatial attention. First, vestibular-induced remission of somatosensory deficits in brain-damaged patients has been proven to be independent of visuo-spatial hemineglect (Vallar *et al.*, 1993). Second, remission of tactile imperception has been described even in a patient affected by a lesion directly involving the primary somatosensory cortex (Bottini *et al.*, 1995). In that patient, the neural correlates of the temporary remission of left hemianesthesia after caloric vestibular stimulation included activations in the right hemisphere (insula, right putamen, inferior frontal gyrus in the premotor cortex). These data have been interpreted as a modulation of somatosensory perception induced by vestibular stimulation and mediated by a right hemispheric neural network putatively involved in somatosensory processing and awareness (Bottini *et al.*, 1995, 2005). In other words, an undamaged subset of ‘sensory body representations’ (cf. Bottini *et al.*, 1995) is able to mediate tactile perception when an appropriate physiological manipulation is introduced. However, this manipulation would need to have sufficient anatomical specificity to reduce the distorted sensory representation caused by the brain lesion. Bottini *et al.* (1995) suggested that shared anatomical projections between vestibular and somatosensory system might be responsible for these effects.

7. Vestibular–Somatosensory Interactions: Vestibular Modulation of Somatosensory Affference

We recently hypothesised a different interpretation of vestibular–somatosensory interactions, based on intermodal gain modulation (Ferrè *et al.*, 2011b, 2013b). Briefly, vestibular inputs would influence the gain of different stages along the somatosensory afferent pathway. This hypothesis can be distinguished from multisensory convergence for sensorimotor control, because there is no transformation of vestibular or somatosensory information into another modality or an amodal format. The hypothesis can be distinguished from non-specific attentional or spatial effects because it proposes modality-specific changes in somatosensory processing (Table 1) (Ferrè *et al.*, 2011a, 2011b, 2013b).

Caloric vestibular stimulation was administered in healthy volunteers to estimate vestibular effects on somatosensory perception (Ferrè *et al.*, 2011b). The detection of faint somatosensory stimuli was estimated using signal detection analysis, to distinguish perceptual sensitivity from response bias. The most striking result was a clear enhancement of perceptual sensitivity by vestibular stimulation. This effect was found for detection of shocks on both left and right hands, i.e., both ipsilateral and contralateral to the side of caloric vestibular stimulation. A visual contrast sensitivity task was administered in the same group of participants during the same testing session to control for non-specific, supramodal effects such as arousal — no such effects were found.

Since caloric vestibular stimulation does not allow precise control of vestibular activation, other studies investigated the vestibular modulation of somatosensory perception using galvanic vestibular stimulation. This involves a weak direct current passing between surface electrodes placed on the mastoid behind the ear (Fitzpatrick and Day, 2004). Although this method is quantitatively well controlled, it evokes rather unspecific pattern of activation in the whole vestibular nerve, mimicking a multidirectional head motion (Goldberg *et al.*, 1984). Crucially, the polarity of stimulation can be reversed as part of the experimental procedure, producing opposite effects on firing rate in the two vestibular nerves, and thus reversing the direction of the virtual rotation vector (Fitzpatrick and Day, 2004). Moreover, placing the galvanic vestibular stimulation electrodes away from the mastoids allows a sham stimulation, producing the same skin sensations under the electrodes as real vestibular stimulation, but without stimulation of the vestibular nerve.

Left anodal/right cathodal galvanic vestibular stimulation selectively improved the ability to detect faint tactile stimuli, confirming previous findings obtained with caloric vestibular stimulation (Ferrè *et al.*, 2013c). This enhancement was found for shocks on both the left and right hand, i.e., both ipsilateral and contralateral to left anodal/right cathodal galvanic vestibular stimulation. Right anodal/left cathodal galvanic vestibular stimulation had no significant effects on tactile perception. Since left anodal/right cathodal galvanic vestibular stimulation mimics a decrease in the firing rate of the vestibular nerve on the left side and an increase on the right side (Goldberg *et al.*, 1984), we suggested that polarity-specific influence on touch could reflect altered somatosensory processing in the right hemisphere. Effects of galvanic vestibular stimulation polarity on perception are well known and wide-ranging. Kerkhoff *et al.* (2011) reported that left anodal/right cathodal galvanic vestibular stimulation reduced tactile extinction in right-hemisphere patients. Utz *et al.* (2011) reported that left anodal/right cathodal galvanic vestibular stimulation reduced rightward bias in line

bisection in neglect patients, while right anodal/left cathodal had minimal effect. Lenggenhager *et al.* (2008) found that response times in a mental transformation task were increased during right but not left anodal galvanic vestibular stimulation for the larger angles of rotation. The disturbing effects of galvanic vestibular stimulation were selectively present in participants who performed egocentric mental transformation and not object-based mental transformation.

This suggestion was consistent with the results of an electrophysiological study in which we recorded somatosensory evoked potentials elicited by left median nerve stimulation immediately both before and again immediately after left ear cold water caloric vestibular stimulation. The results showed a vestibular-induced modulation in the N80 component over both ipsilateral and contralateral somatosensory areas (Ferrè *et al.*, 2012). The vestibular modulation was specific to this component, since neither earlier nor later somatosensory evoked components were affected. Moreover, the effect was also specific to somatosensory processing: visual evoked potentials to reversing checkerboard patterns were not influenced by caloric vestibular stimulation, ruling out explanations based on indirect vestibular effects mediated by general arousal or supramodal attention.

Critically, the N80 component has been localised in the parietal operculum (area OP 1—Eickhoff *et al.*, 2010; Jung *et al.*, 2009), which functionally corresponds to the secondary somatosensory cortex (Eickhoff *et al.*, 2010). Moreover, the vestibular-induced modulation had similar amplitude contralaterally and ipsilaterally (Jung *et al.*, 2009). This strongly supports the hypothesis of an origin for this somatosensory component in the secondary somatosensory cortex, given the bilateral organisation of this area (Iwamura *et al.*, 1994). The secondary somatosensory cortex from which N80 is assumed to arise is immediately adjacent to the neuroanatomical site of vestibular–somatosensory convergence in the human homologue of the monkey PIVC, identified as OP 2 by Zu Eulenberg *et al.* (2012). OP 2 lies slightly deeper within the Sylvian fissure than OP 1, at the junction of the posterior parietal operculum with the insular and retroinsular region (Eickhoff *et al.*, 2006a, b).

Caloric and galvanic vestibular stimulation influence both low-level perceptual and higher-level attentional functions (Figliozzi *et al.*, 2005). Indeed, neuroimaging studies show vestibular activations in anterior parietal areas traditionally linked to somatosensory perception, and more posterior parietal areas traditionally linked to multisensory spatial attention (Bottini *et al.*, 1994, 1995). Therefore, disentangling perceptual from spatial-attentional components of vestibular–somatosensory interaction is problematic. However, natural vestibular stimulation from whole-body rotations offers one way of doing this,

because of uncontested physical directionality of the vestibular signals. For example, *ceteris paribus*, if the body is rotated towards the left, modulation of somatosensation on the left hand might be either perceptual or spatial-attentional, whereas modulation of somatosensation on the right hand could only be perceptual (Ferrè *et al.*, 2014; Figliozzi *et al.*, 2005). Accordingly, we investigated whether *natural* vestibular activation induced by passive whole-body rotation would also influence somatosensory detection, by measuring tactile detection during whole body rotation (Ferrè *et al.*, 2014). We found that passive whole-body rotations significantly enhanced sensitivity to faint shocks to both left and right hands, without affecting response bias. Crucially, there was no significant spatial congruence effect between the direction of rotation and the hand stimulated, suggesting that the spatial-attentional component may be relatively minor. Thus, our results support a multimodal interaction at the perceptual, rather than attentional level. This effect could arise because of convergence of vestibular and somatosensory signals on bimodal neurons. Other studies, however, did find spatial congruence effects in natural vestibular rotation, though using rather different tasks. Figliozzi *et al.* (2005) administered temporal order judgement tasks for bimanual tactile stimuli during chair rotation. They found a bias to perceive touch earlier on the hand corresponding to the direction of chair rotation, leading to a spatial congruence effect.

Taken together, these results suggest that vestibular–somatosensory links have important effects on perception. These effects may be related to, or caused by, the neuroanatomical overlap or co-location of brain activations seen in neuroimaging studies. However, we have shown that they are distinct from vestibular driving of a supramodal attentional system (Macaluso and Driver, 2005). What might be the functional meaning of these interactions? We have shown that they go beyond a mere multimodal convergence for motor control. We speculate that somatosensory gain modulation is a functional corollary of the vestibular signalling of a new orientation with respect to the environment. With each new orienting movement sensitive pickup of information from novel environments becomes important, and is therefore prioritised. Thus, vestibular signalling of head rotation during orienting movements could trigger increased ability to detect somatosensory stimuli, so as to regulate the relation between the organism and the external environment.

7.1. One Vestibular–Somatosensory Interaction or Two? Effects of Vestibular Stimulation on Touch and Pain

Somatosensory perception refers to information about the body, rather than information about the external world (e.g., vision, hearing or olfaction). Importantly, the somatosensory system processes information about several submodalities of somatic sensation (touch, temperature, pain, etc). We therefore hypothesised that vestibular signals could have dissociable effects on the various different channels *within* the somatosensory system.

A reduction of chronic pain by means of caloric vestibular stimulation has been demonstrated (McGeoch *et al.*, 2008a, b; Ramachandran *et al.*, 2007). At least two alternative mechanisms have been suggested to explain these effects (McGeoch *et al.*, 2008a, b; Ramachandran *et al.*, 2007). First, pain relief may be caused by activation of the thermosensory cortex in the dorsal posterior insula adjacent to PIVC stimulated by the vestibular stimulation. Alternatively, the PIVC itself may be part of the interoceptive system and have a direct role in pain control.

We recently administered caloric vestibular stimulation paradigm in healthy participants and we estimated the psychophysical thresholds for tactile detection and for contact-heat pain, and revealed a vestibular-induced enhancement of touch, but reduction in levels of pain (Ferrè *et al.*, 2013b). However, these results are consistent with either of two possible *neural* models of vestibular–somatosensory interaction. In the first model, a common vestibular input has effects on *independent* systems coding for touch and for pain. Crucially, on this model there is no direct interaction between touch and pain: they are simply driven by a single input. In a second model, vestibular input has a direct effect on touch, but only an indirect effect on pain. The indirect effect could be due to inhibitory links between cortical areas coding for touch and pain: increased activation of somatosensory areas due to vestibular input could, in turn, cause decreased afferent transmission in pain pathways, because of the known tactile ‘gating’ of pain (Melzack and Wall, 1965). To compare the first and second models, we assessed the effects of caloric vestibular stimulation on thresholds for detecting radiant heat pain, evoked by laser stimulation of A δ afferents, without touching the skin (Ferrè *et al.*, 2013b). Vestibular inputs increased the detection threshold of pure nociceptive thermal stimuli (i.e., A δ nociceptors). This pattern of results supports the first model, and cannot simply reflect vestibular-induced response bias, or non-specific effects such as arousal, habituation, or perceptual learning.

A striking feature of vestibular–somatosensory interactions, therefore, is the independent modulation of distinct somatosensory submodalities, such as touch and pain. Decreases in tactile threshold demonstrate an up-regulation of tactile processing, while increases in pain threshold demonstrate a down-regulation of nociceptive processing. The

vestibular system thus modulates connections with different somatosensory submodalities, regulating the activity in multiple sensory systems independently. Human neuroimaging studies support this model, showing that vestibular stimulation both increases somatosensory cortex activations (Bottini *et al.*, 1994, 1995; Emri *et al.*, 2003; Fasold *et al.*, 2002), but deactivates visual cortex (Bense *et al.*, 2001). The secondary somatosensory cortex seems a good candidate for such interactions. Interestingly, this area plays a major role in both touch and pain perception (Ploner *et al.*, 1999).

However, the effects of vestibular signals on pain processing are less well understood, and potentially involving effects at multiple different levels of nociceptive processing (cf. Ferrè *et al.*, 2013b, and McGeogh *et al.*, 2008b). A systematic investigation of the basis of this modulation is necessary to clarify the neural and functional correlates of these interactions.

8. A Functional Model for Vestibular–Somatosensory Interactions

The evidence reviewed above suggests pervasive interactions between the vestibular and somatosensory systems. In this section, we summarise these interactions in a functional model (see Fig. 1). Any organism moving through its environment, and interacting with it by whole body navigational movements and reaching movements, receives a constant stream of both vestibular and somatosensory inputs. These will interact at several levels of input.

First, and perhaps trivially, they will interact through the physical environment. Movements of the body are physical events transduced by both vestibular and somatosensory systems, so strong vestibular–somatosensory correlations are expected. In addition, vestibular signals drive postural reflexes, which trigger characteristic somatosensory inputs. For instance, vestibular-driven balance responses cause somatosensory afference from the feet.

Moreover, the vestibular and somatosensory systems interact within the central nervous system, even in the absence of any physical movement of the body. We have presented evidence for *direct* effects of vestibular signals on somatosensory perception. These effects can be described as vestibular modulations of the gain in somatosensory processing pathways. These direct interactions appear to involve convergence of vestibular signals on somatosensory cortical areas, possibly through bimodal vestibular–somatosensory neurons. We speculate that this form of direct vestibular–somatosensory interaction within the brain could facilitate optimal sensing of the environment. For example, vestibular signalling of

head rotation during movements enhances the ability to detect somatosensory stimuli, so as to regulate the relation between the organism and the external environment.

Finally, vestibular–somatosensory interactions also occur because of *indirect* links via high-level cognitive processes, notably spatial attention. In this case vestibular signals do not directly influence somatosensory processing. Rather vestibular inputs trigger changes in amodal spatial attention, which in turn influences somatosensory system performance.

What is the consequence of these interactions? We speculate that vestibular–somatosensory interaction makes an important contribution to one form of self-representation, namely the sense of one's body as a stable and coherent object. In particular, vestibular signals allow the barrage of sensory afferences to be parsed into those that are due to self-motion within the environment (i.e., correlate with vestibular signals), and residual afferences that are not. Residual afferences that are not related to vestibular-signalled self-motion represent the stable, consistent features of the body that remain the same as we move through the world. In Gestalt psychology, elements that move coherently are perceived as more related than elements that do not. As a result of this *principle of common fate*, the coherent visual motion of a number of dots in a random dot kinematogram can readily define a visual object that is invisible in any single static frame of the same kinematogram (Uttal *et al.*, 2000). Similar mechanisms have been identified in other sensory modalities (Gallace and Spence, 2011). The vestibular–somatosensory interaction amounts to a common fate for self-representation. Imagine our organism exploring the environment by sliding down a hill, and receiving tactile inputs from contact between the skin and the bumpy hillside as it slides. The population of all sensory afferent signals is divided into two classes. One rapidly varying set of signals correlates with vestibular signals of head rotation and acceleration. This reflects the somatosensory signals elicited by the contact with the environment. The remaining set of signals is consistent and coherent with each other, but relatively independent of the vestibular motion. These residual signals are sensations reflecting the continuous state and presence of the body, independent of current action, movement, and interaction with the environment. The vestibular signal plays the key role in distinguishing the coherent, unified, persisting body from the contingencies of its momentary interactions with the world. Interestingly, cortical vestibular dysfunction leads to disintegration in the normal unity of the self. For example, in cases of autoscopic phenomena, patients with damage to vestibular brain areas may localise the self outside their own body and may experience seeing their body from this disembodied perspective (Blanke and Mohr, 2005). In depersonalisation/derealisation phenomena, the normal sense of familiarity with one's own body is lost (Sang *et al.*, 2006).

9. Conclusion

The vestibular system provides fundamental signals about the position and motion of the body, relative to the external environment. Despite the highly specialized nature of the peripheral components of the vestibular system, no unimodal vestibular cortex has been identified in the human brain. Instead, several multimodal sensory areas integrate vestibular, visual and somatosensory signals. Here we have argued that vestibular signals are not only an input for motor control and postural responses, but also a distinct form of information about one's own body. In particular, we have proposed that the target representation of vestibular–somatosensory interactions is a form of self-representation. This representation has the role of linking the spatial description of one's own body to the spatial description of the outside world. Interaction between vestibular signals and somatosensory inputs might play the key role in distinguishing the coherent, unified body from the contingencies of its momentary interactions with the world.

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Conflict of interest

The authors declare no competing financial interests.

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Figure caption

Figure 1. A functional model for vestibular–somatosensory interaction. See text for explanation.

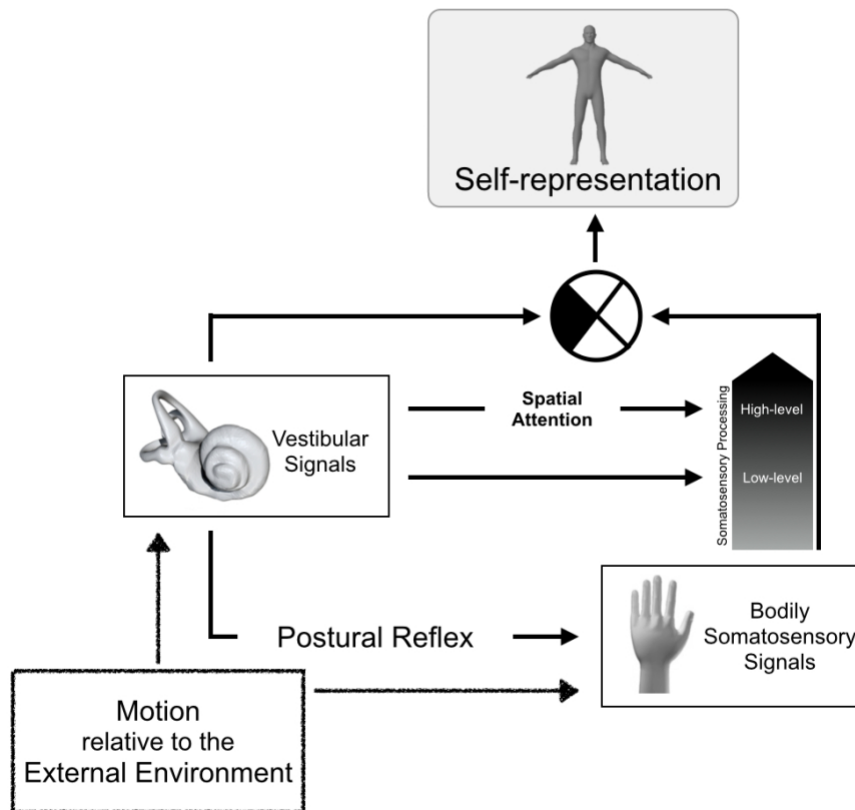


Table 1. Vestibular modulation of touch: behavioural evidence. Summary of behavioural effects elicited by vestibular stimulation on somatosensory perception in brain damaged patients and healthy participants. CVS: caloric vestibular stimulation; LA/RC GVS: left anodal and right cathodal galvanic vestibular stimulation; RA/LC GVS: right anodal and left cathodal galvanic vestibular stimulation; RBD: right brain damaged patients; LBD: left brain damaged patients; HP: healthy participants; TOJs: temporal order judgments; SEPs: somatosensory evoked potentials.

Study	Vestibular stimulation	Group	Task	Behavioural effects
Vallar <i>et al.</i> 1990	Left ear cold CVS	RBD	Tactile detection	Remission of left side hemianaesthesia
Vallar <i>et al.</i> 1993	Left ear cold CVS	RBD	Tactile detection	Remission of left side hemianaesthesia and tactile extinction
	Right ear cold CVS	LBD	Tactile detection	No effects
Bottini <i>et al.</i> 1995	Left ear cold CVS	RBD	Tactile detection	Remission of left side hemianaesthesia
Bottini <i>et al.</i> 2005	Left ear cold CVS	RBD	Tactile detection	Remission of left side hemianaesthesia
	Right ear cold CVS	LBD	Tactile detection	No effects
	Left ear cold CVS	LBD	Tactile detection	Remission of right side hemianaesthesia
Figliozzi <i>et al.</i> 2005	Passive whole body rotation	HP	TOJs	Spatial congruency effects on touch
Kerkhoff <i>et al.</i> 2011	LA/RC GVS	RBD	Tactile extinction	Remission of left side tactile extinction (identical stimuli)
	RA/LC GVS	RBD	Tactile extinction	Remission of left side tactile extinction (different stimuli)
Ferrè <i>et al.</i> 2011a	Left ear cold CVS	HP	Tactile detection	Increase in detection rate
Ferrè <i>et al.</i> 2011b	Left ear cold CVS	HP	Tactile detection	Increase in tactile sensitivity
Ferrè <i>et al.</i> 2012	Left ear cold CVS	HP	SEPs	Modulation of N80 SEPs component
Schmidt <i>et al.</i> 2013	LA/RC GVS	RBD	Tactile extinction	Remission of tactile extinction (identical and different stimuli)
	RA/LC GVS	RBD	Tactile extinction	Remission of tactile extinction (identical and different stimuli)
Ferrè <i>et al.</i> 2013b	Left ear cold CVS	HP	Touch/Pain threshold	Decrease in tactile threshold, increase in pain threshold
Ferrè <i>et al.</i> 2013c	LA/RC GVS	HP	Tactile detection	Increase in tactile sensitivity
	RA/LC GVS	HP	Tactile detection	No effects

Ferrè <i>et al.</i> 2014	Passive whole body rotation	HP	Tactile detection	Increase in tactile sensitivity, no spatial congruency effects
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